
SYSTEMATICS AND TAXONOMY OF ISLAND AND MAINLAND POPULATIONS OF WESTERN HARVEST MICE (*REITHRODONTOMYS MEGALOTIS*) IN SOUTHERN CALIFORNIA

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ABSTRACT. Western harvest mice (*Reithrodontomys megalotis*) are classified into four subspecies in southern California. Samples from three California islands and 14 mainland localities from the Santa Ynez River to the Mexican border were examined for patterns of geographic variation, using morphometrics and allozymes. The sample from Santa Catalina Island is the most divergent, but even so, it can be considered to have colonized the island in the Holocene. Western harvest mice probably were introduced inadvertently to Santa Cruz and Santa Catalina islands by Indians, whereas the San Clemente populations probably were introduced by Europeans sometime in the last 100 years. On the mainland, patterns of variability do not exhibit geographic trends, nor do they correspond to presently accepted taxonomic classification. Based on these results, only one subspecies of western harvest mouse is recognized in coastal southern California, and *R. m. catalinae*, *R. m. limicola*, and *R. m. santacruzae* are relegated to synonymy under *R. m. longicaudus*.

INTRODUCTION

The western harvest mouse (*Reithrodontomys megalotis*) has the widest geographic distribution of all North American harvest mice, ranging from southwestern Canada (British Columbia east to Saskatchewan) southward into southern Mexico (Oaxaca and Veracruz) and from California east into recently invaded Indiana (Ford, 1977; Hall, 1981; Webster and Jones, 1982). Probably because of this wide geographic distribution, *R. megalotis* exhibits a moderate amount of intraspecific variation in morphological characters, and at present 16 subspecies are recognized (Webster and Jones, 1982). Within this broad geographic range, western harvest mice have been found in a variety of habitats and elevations. These mice have been recorded from below sea level at Death Valley to above 3960 meters in southern Mexico (Webster and Jones, 1982). In California, western harvest mice tend to inhabit grassy and weedy habitats such as meadows, fence rows, fallow fields, overgrown pastures, coastal salt

marshes, and borders of agricultural and riparian areas (Grinnell, 1933; Webster and Jones, 1982).

With the exception of Howell (1914), there has been no extensive effort made to study the systematics of this species over its entire range. Original descriptions for most of the subspecies were based on small samples composed of individuals of various ages, and the taxonomic legitimacy of some of these subspecies is in question. A few authors have conducted systematic studies over portions of the species' range. Fisler (1965) studied intraspecific variation in populations of *R. megalotis longicaudus* from the San Francisco Bay area. He found no appreciable sexual dimorphism and little local geographic variation in the six samples examined. Using only univariate statistical methods, Hoffmeister and Warnock (1955) reevaluated the taxonomic status of western harvest mice from the Midwest, whereas Jones and Mursaloglu (1961) studied geographic variation in western harvest mice on the central Great Plains. Hoffmeister (1986) examined and reported on the taxonomic status of western harvest mice from Arizona. In each of these studies, *R. megalotis* showed no significant sexual dimorphism and little intraspecific variation, and the authors relegated several previously described subspecies to synonymy with other forms. There has been no attempt to study geographic variation in western harvest mice using both allozymic and morpho-

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metric data with univariate and multivariate statistical methods.

Hall (1981) and Webster and Jones (1982) currently recognize six subspecies of *R. megalotis* in California (*longicaudus*, *megalotis*, *distichlis*, *limicola*, *catalinae*, and *santacruzae*). West of the Sierra Nevada and Mojave Desert is a widespread, grassland form of harvest mouse, first described as *Reithrodon longicauda* by Baird (1857), but later relegated by Howell (1914) to subspecific status as *R. m. longicaudus* under the widespread species *R. megalotis*. North and east of the Sierra Nevada in the Great Basin and throughout much of the Colorado and Mojave deserts is the nominotypical subspecies. Von Bloeker (1932, 1937) described *R. m. limicola* from the salt marshes of southern California from Point Mugu, Ventura County, to Newport Bay, Orange County (Williams, 1986) and *R. m. distichlis* from the coastal salt marshes and sand hills from Elkhorn Slough to Seaside Lagoon in Monterey County. Both of these subspecies were characterized as having darker coloration than adjacent upland western harvest mice. Although Fisler (1965) found a similar tendency to dark pelage color in western harvest mice inhabiting salt marshes in the San Francisco Bay area, he did not feel that this character was sufficient to warrant subspecific classification for those populations. Pearson (1951) could not find differences between *R. m. distichlis* and *R. m. longicaudus*, and in preliminary analyses, we could find no significant morphological or allozymic evidence to support the continued recognition of *R. m. limicola* in southern California. Therefore, the taxonomic status of populations of western harvest mice in California is in need of review.

Western harvest mice have been found on three of the California islands: San Clemente, Santa Catalina, and Santa Cruz. According to von Bloeker (1967), the harvest mice on San Clemente Island were introduced from populations of *R. m. longicaudus* from the adjacent mainland, but until now, the taxonomic affinities of the San Clemente Island population have not been examined thoroughly. The Santa Catalina Island form was originally described as *Rhithrodontomys (sic) catalinae* (Elliot, 1904) but was later relegated to subspecific status as *R. m. catalinae* (Grinnell, 1913; Hooper, 1952). Harvest mice were discovered on Santa Cruz Island in 1948 and were described by Pearson (1951) as *R. m. santacruzae*. Both of the island subspecies can be differentiated from adjacent mainland taxa on the basis of their larger size (Elliot, 1904; Pearson, 1951), but they were described on the basis of only a few specimens.

Few studies have been published on genic variability within *R. megalotis*. Arnold *et al.* (1983) examined 20 presumptive loci in a sample of 13 individuals from Arkansas, California, Kansas, New Mexico, and Tlaxcala; only three loci were variable. Nelson *et al.* (1984) examined 30 isozymes in a sample of seven individuals from California, Kan-

sas, and Texas and, again, found only three loci to be variable. No work has been published examining genic variability within or among large samples of western harvest mice.

Our objectives are to (1) reevaluate the taxonomic status of coastal salt marsh and island populations of *R. megalotis* in southern California using both allozymic (electrophoretic) and morphometric characters; (2) determine whether the patterns of morphologic and genic variation are concordant in these populations; (3) develop explanations for the patterns of differentiation observed by examining the possible underlying causes; (4) determine the extent that subspecies of harvest mice in southern California represent the kind of evolutionary unit espoused by present-day systematists (*e.g.*, Barrowclough, 1982; Monroe, 1982; Thorpe, 1987); (5) examine the possibility that one or more of the island populations were purposefully or accidentally introduced by humans; and (6) test the hypothesis that populations of *R. megalotis* from coastal salt marshes in southern California are contiguous with, and have diverged little from, adjacent upland populations.

METHODS

ALLOZYMIC ANALYSES

For the allozyme analyses, 208 individuals were examined. Specimens were assigned to 15 samples (Fig. 1); sample sizes and localities are listed in the Appendix. Heart, liver, and kidneys were taken from each specimen at death and stored at -70°C until processed; in a few cases, tissues were removed from animals frozen at -5°C for several weeks (George, 1988). Tissue preparation (heart and kidneys were processed together), horizontal starch-gel electrophoresis, and biochemical staining procedures were modified from techniques described by Selander *et al.* (1971). Wherever possible, NAD-dependent glucose-6-phosphate dehydrogenase (G-6-PDH) was substituted for NADP-dependent G-6-PDH as a cost-saving measure (Buth and Murphy, 1980). Gels were prepared from Connaught starch. Buffer systems were those of Selander *et al.* (1971), as follows: I—continuous tris-citrate I (3.5 hr, 150 V, heart and kidneys), II—continuous tris-citrate II (5 hr, 130 V, liver), III—phosphate (4 hr, 130 V, liver). Thirty presumptive loci were examined (acronyms and buffer systems in parentheses): albumin (AB; I), hemoglobin (HB; I), lactate dehydrogenase (LDH-1, LDH-2; I), glucose-phosphate isomerase (GPI; I), isocitrate dehydrogenase (ICD; I), peptidase A (glycyl-leucine, Pep-A; I), peptidase B (leucyl-glycyl-glycine, Pep-B; I), peptidase D (phenylalanyl-proline, Pep-D; I), malic enzyme (ME; I), malate dehydrogenase (MDH-1, MDH-2; I), sorbitol dehydrogenase (SDH; I), superoxide dismutase (SOD; II), α -glycerophosphate dehydrogenase (α -GPD; II), alcohol dehydrogenase (ADH; II), glutamate oxaloacetate dehydrogenase (Got-1, Got-2; II), esterase (Est-1, Est-2; II), purine nucleoside phosphorylase (NP; III), phosphoglucomutase (PGM; I), adenylate kinase (AdK; I), creatine kinase (Ck-1, Ck-2; III), glucose-6-phosphate dehydrogenase (G6PDH; I), 6-phosphogluconate dehydrogenase (6-PGD; I), diaphorase (Dia; III), adenosine deaminase (ADA; III), leucine amino peptidase (LAP; II). Alleles for each locus were designated alphabetically, beginning with

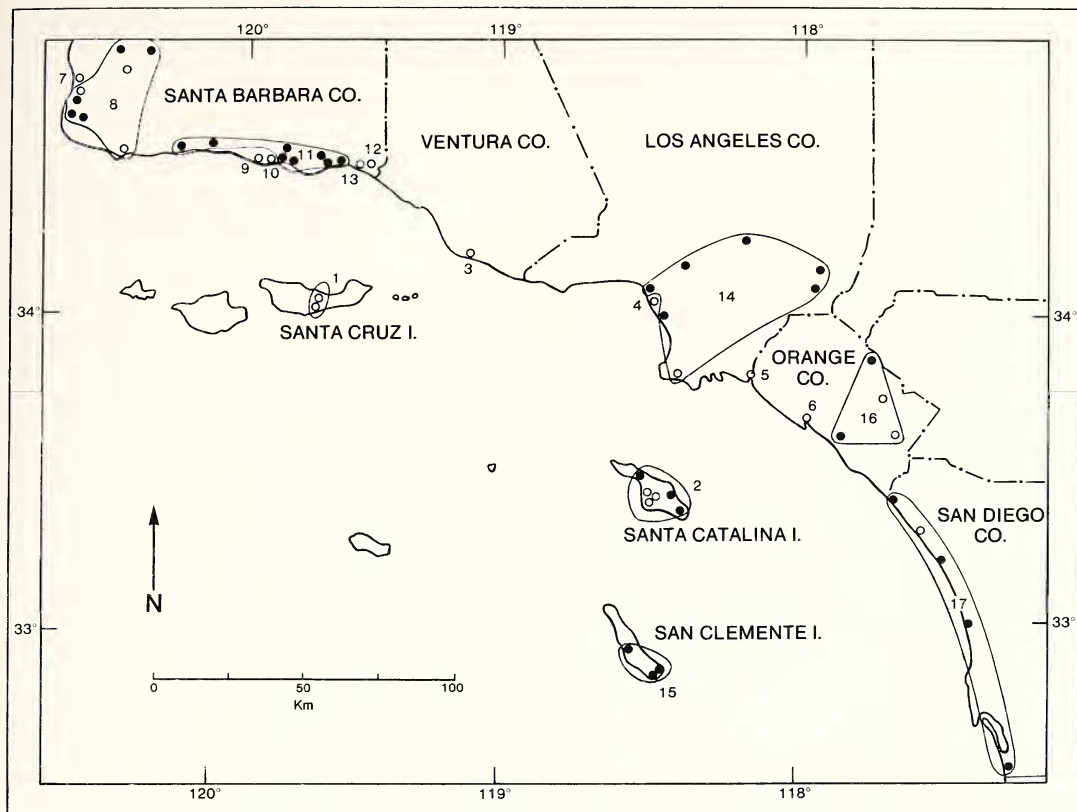


Figure 1. Map of sample localities. Closed dots denote localities where individuals were used only in morphometric analyses; open dots mark localities included in both morphometric and allozymic analyses. Numbers refer to the following samples: (1) SCRUI, (2) SCATI, (3) PTMUGU, (4) DELREY, (5) ANAHM, (6) NEWPRT, (7) STYNEZ, (8) NSBARB, (9) DEVERO, (10) GOLETA, (11) SSBARB, (12) CARPUP, (13) CARPIN, (14) LACOU, (15) SCLEMI, (16) ORANGE, (17) SDIEGO. Acronyms are defined and localities are listed in the Appendix.

the most anodal position. Allozymes that migrated cathodally were designated with a negative sign. Side-by-side comparisons of mobilities of allozymes on the same gel were used for comparison of alleles.

Allelic frequencies, estimates of mean heterozygosity (H), and percent loci polymorphic (P) were calculated for each species. Matrices of Nei's (1972) identity and Rogers' (1972) similarity and distance were generated from the genic data. Cluster analysis of Nei's distance matrix was performed with the unweighted pair-group method using arithmetic means (UPGMA) of BIOSYS-1 (Swofford and Selander, 1981). The distance-Wagner procedure (DISWAG of BIOSYS-1 with addition criteria III and rooted at the midpoint) was employed with Rogers' distance matrix. F -statistics were calculated to apportion the total genetic variation into inbreeding coefficients within populations (F_{IS}) and within the total population (F_{IT}) and into allelic variance among populations (F_{ST}), using the FSTAT step of BIOSYS-1 (Nei, 1977; Swofford and Selander, 1981).

MORPHOMETRIC ANALYSES

A total of 457 western harvest mice from 14 mainland and three island samples in southern California (Fig. 1) were examined for morphometric analyses. The samples are similar to those included in the allozymic study, with

the exception of samples 11 (southern Santa Barbara County) and 15 (San Clemente Island) for which we had no tissues. Sample sizes and localities for specimens used in the final data set are listed in the Appendix. Fourteen cranial measurements were taken from each specimen (Fig. 2), following the methods described in Hooper (1952) and Fislre (1965) unless otherwise indicated: greatest length of skull (GL), breadth of braincase (BB), length of braincase (LBC, measured from the leading edge of the shallow notch on the superior orbital border of the zygomatic arch to the occipital condyle), zygomatic breadth (ZB), breadth of rostrum (BR), depth of braincase (DBC, measured by resting the calipers on the basisphenoid and basioccipital sutures and measuring to the dorsal surface of the cranium), intermeatus width (IMW, the least distance between the bullae measured at the basioccipital suture), length of rostrum (LR, measured from the leading edge of the shallow notch on the superior orbital border of the zygomatic arch to the tip of the nasals), length of nasals (LN), length of incisive foramen (LIF), length of molar toothrow (AL), interorbital breadth (IB), length of palate (LP, measured from the posterior edge of the alveoli of the incisors to the mesopterygoid fossa), breadth of zygomatic plate (BZP). The first six measurements were taken with dial calipers to the nearest 0.01 mm, whereas the remaining eight measurements were taken with an ocular micrometer to the nearest 0.1 mm. Specimens lack-

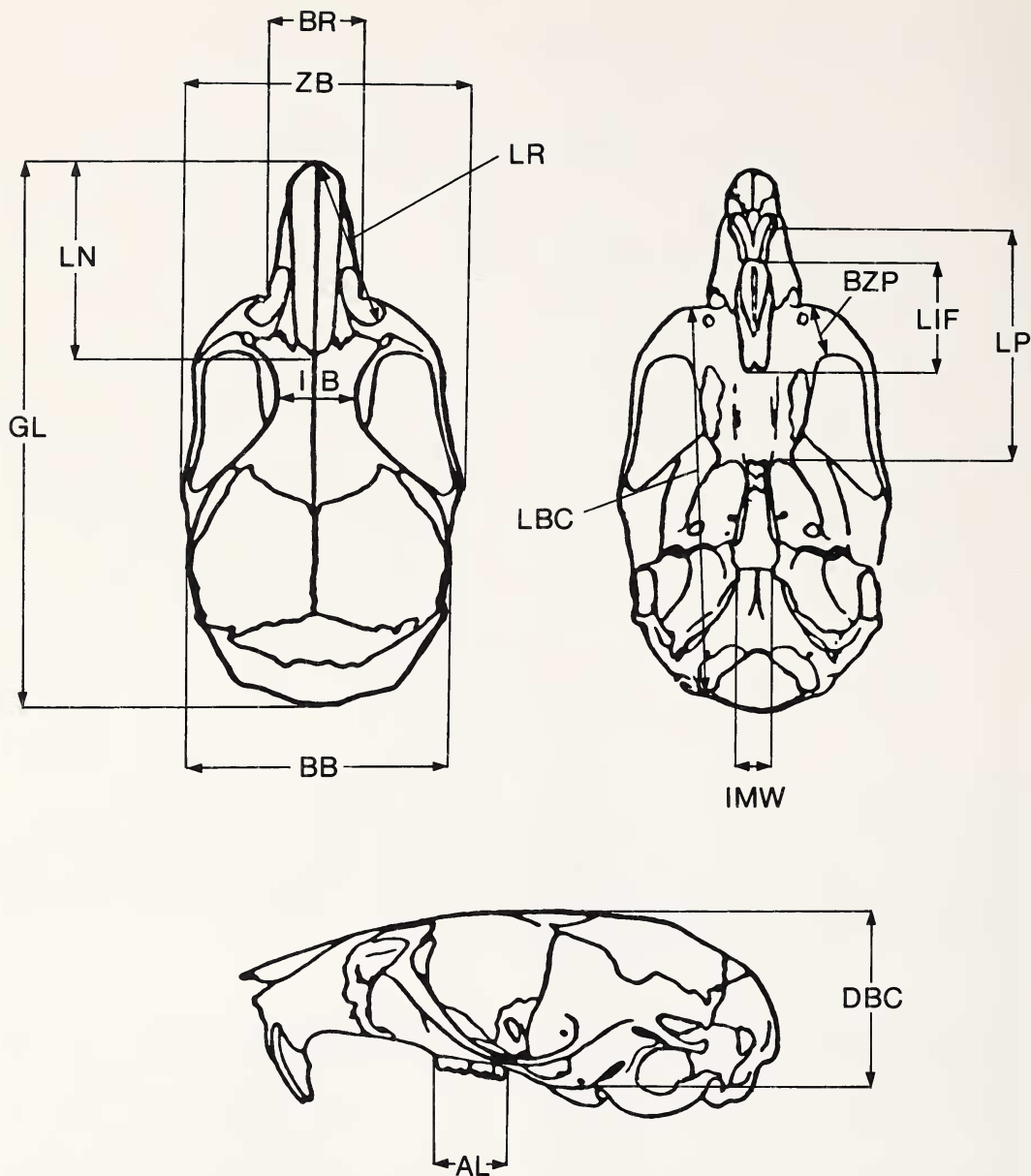


Figure 2. Fourteen cranial measurements used in this study; acronyms are defined and described in the Methods section.

ing one or more measurements were excluded from the analyses.

Specimens were assigned to one of six age categories based on wear of the upper molars. The categories correspond to the age classes described by Fisler (1965) except where noted as follows: juvenile (class 1 of Fisler [1965]), subadult (class 2), young adult (class 3), adult (class 4; and confluent dentine canal connecting the protocone, paracone, and metacone [Hoffmeister, 1986]), middle-aged adult (class 5), old adult (class 6).

Using BIOSTAT I, univariate statistics were calculated for all samples and variables; tests of normality, Student-Newman-Keuls (SNK) multiple range tests, and analyses of variance were obtained using BIOSTAT II (Pimentel and Smith, 1986a, b). To examine the extent of secondary

sexual variation in *R. megalotis*, the 14 cranial measurements for males and females were compared from one island sample (Santa Catalina, sample 2) and three mainland samples (Santa Barbara County upland combined, samples 8 and 11; Goleta and Devereux sloughs combined, samples 9 and 10; and Point Mugu, sample 3), using *t*-tests (BIOSTAT I; Pimentel and Smith, 1986a). Ontogenetic variation was studied by comparing means of the 14 cranial variables among age classes for the Santa Catalina Island sample and the northern and southern Santa Barbara County upland samples combined. Methods used were the SNK multiple range tests to determine the maximal nonsignificant subsets and *F*-tests (BIOSTAT II; Pimentel and Smith, 1986b).

Based on results of the studies of secondary sexual and

ontogenetic variation, we elected to combine sexes and age classes 2–6 for all samples (see Results section). Tests of normality indicated that three variables (BB, IB, and BZP) exhibit significant departures from normality, being negatively skewed and highly leptokurtotic. These variables were excluded from the multivariate analyses. Despite slight leptokurtosis, BR and LR were included. Multigroup discriminant function analysis was performed using BIOSTAT II (Pimentel and Smith, 1986b).

RESULTS

ALLOZYMIC VARIATION

Of the 30 loci examined, 10 were fixed for a single allele across the 15 samples, and 20 were polymorphic in at least one sample (Table 1). Unique alleles were detected in nine populations: SCATI (Pep-A^A, Ck-2^{-B}), DELREY (α -GPD^C), ANAHEM (ME^B), STYNEZ (Pep-A^B, 6-PGD^C), GOLETA (G6PDH^A), DEVERO (GPI-A^A, DIA^A), CARPIN (Pep-A^D, NP^A), CARPUP (6-PGD^D), SDIEGO (6-PGD^B). With the exception of Ck-2^{-B} in population SCATI, the unique alleles exist at low frequencies.

Geographic patterns of variation may be discerned for a few loci. For LDH-2, allele A appears at low levels in southern populations only (ANAHEM, LACOU, SDIEGO). Allozyme B at ADH appears in the three southernmost populations (NEWPR, ORANGE, SDIEGO) but also shows up at PTMUGU; a similar pattern is seen for allozyme B at Got-1, which also is seen in another southern population (LACOU). Interestingly, allele A at ADA is found in both island samples and in every population from PTMUGU south, with the exception of sample ORANGE. The populations assigned to *R. m. limicola* do not differ appreciably from populations assigned to *R. m. longicaudus* when patterns of geographic variation in single loci are examined. There are no fixed differences at any loci, and with two exceptions, the common allele for each locus is the same for all populations. For the sample from Santa Catalina Island, allele B (rather than C) is in the highest frequency at Pep-D, and allele A (rather than B) is in the highest frequency at ADA.

Mean heterozygosity (H) within populations ranges from 0.03 to 0.08 (Table 2) (mean = 0.04 across all samples). Using the 0.95 criterion (*i.e.*, excluding loci for which the common allele is at a frequency above 0.95), polymorphism within populations varies from 6.7 to 26.7%, whereas using the 0.99 criterion, polymorphism varies from 10 to 26.7%. The latter values are identical to values calculated using no criterion at all (*i.e.*, including all polymorphic loci, regardless of allelic frequency). Across all samples, polymorphism is 13.3% using the 0.95 criterion, 36.7% using the 0.99 criterion, and 66.7% using no criterion at all.

F -statistics averaged across all loci and all populations sampled were $F_{IS} = 0.245$, $F_{IT} = 0.307$, and $F_{ST} = 0.081$. In other words, only 8.1% of the total genetic variation found in these populations may be ascribed to among population variation.

The average inbreeding coefficient within samples is 0.245, whereas the inbreeding coefficient among samples is 0.307.

The UPGMA phenogram (Fig. 3) of Nei's distance matrix shows all populations clustering below the 2.3% level. The cophenetic correlation coefficient of the phenogram is 0.917, indicating that little distortion of the distance values was necessary to construct the tree. UPGMA clustering of the identity matrix yielded a tree with identical topology and a cophenetic correlation coefficient of 0.952. The first population to diverge is that from Santa Catalina Island; the second is that from Newport Bay, at the 1.4% level. The remaining populations cluster at or below the 0.7% distance. No recognizable patterns that correspond to geography or taxonomic subdivisions can be discerned from the clustered samples. There are no obvious north-south clines, and although three of the four populations attributed to the marshland subspecies, *R. m. limicola* (DELREY, ANAHEM, PTMUGU), are together, they are clustered with the sample from Santa Cruz Island. The fourth population classified as *R. m. limicola* (NEWPR) is the second-most divergent sample examined.

The distance-Wagner tree (Fig. 4), rooted at the midpoint, has a cophenetic correlation coefficient of 0.904 and shows a pattern of clustering similar to that seen in both UPGMA phenograms. There are neither north-south nor wetland-upland patterns of clustering. Samples from Santa Catalina Island and Newport Bay have the greatest branch length. This may be explained by the sample from Newport Bay having the highest rate of heterozygosity (0.08) and the sample from Santa Catalina Island having unusual allele frequencies at two loci, Pep-D and ADA (Table 1).

MORPHOLOGIC VARIATION

Summary statistics (mean, range, standard deviation, and coefficient of variation), results of Student-Newman-Keuls multiple range tests, and analysis of variance for each of the 11 cranial characters are shown in Table 2. Analysis of variance revealed highly significant differences ($P < 0.001$) among samples for each character.

Nongeographic Variation

Sexual Variation. Males average larger than females in each of the four samples tested for only four measurements (GL, DBC, IW, LIF), whereas females are larger in four measurements (LR, AL, BR, BZP). These differences are not statistically significant ($P > 0.05$). The remaining six measurements show no consistent pattern in sexual dimorphism across the four samples. Only IW, BR, and BZP show statistically significant ($P < 0.0001$) differences between the sexes, but the dimorphism is significant for each measurement in only one of the four samples (IW in sample 8/11, BR in sample 9/10, BZP in sample 3). Because none of the 14

Table 1. Electromorphs, mean heterozygosity (*H*), percent polymorphism (*P*) (95% and 99% criteria), and *F*-statistics for 20 polymorphic loci scored across 15 populations of *Reithrodontomys megalotis* in southern California. Allelic designations are described in text. Where a locus is polymorphic within a population, allelic frequencies are given in parentheses.

Sample	n	LDH-2	GPI	ICD	Pep-D	Pep-B	Pep-A	ME
SCRUZI	20	B	—B	C	C	B	C	A
SCATI	15	B	—B	A (0.03) C (0.97)	B (0.67) C (0.33)	B	A (0.07)* C (0.93)	A
PTMUGU	20	B	—B	C (0.97) D (0.03)	A (0.05)† B (0.25) C (0.70)	B	C	A
DELREY	15	B	—B	C	B (0.13) C (0.70)	B	C	A
ANAHAM	15	A (0.07) B (0.93)	—B	C	A (0.10)† B (0.13) C (0.77)	A (0.13) B (0.87)	C	A (0.93)* B (0.03)
NEWPRT	11	B	—B	C	A (0.09) B (0.41) C (0.50)	B	C	A
STYNEZ	18	B	—B	B (0.03) C (0.97)	B (0.28) C (0.72)	B	B (0.03) C (0.97)	A
NSBARB	14	B	—B	C	C	B	C	A
DEVERO	13	B	—A (0.04) —B (0.96)	C	B (0.12) C (0.88)	A (0.04) B (0.96)	C	A
GOLETA	13	B	—B	A (0.04)* B (0.08) C (0.88)	A (0.08)† B (0.31) C (0.61)	A (0.04) B (0.96)	C	A
CARPUP	12	B	—B	C	B (0.38) C (0.62)	B	C	A
CARPIN	14	B	—B	C	B (0.07)* C (0.93)	B	C (0.96) D (0.04)	A
LACOU	11	A (0.09)* B (0.91)	—B	C	B (0.18) B (0.82)	B	C	A
ORANGE	10	B	—B	C	B (0.05) C (0.95)	B	C	A
SDIEGO	7	A (0.07) B (0.93)	—B	C (0.93) D (0.07)	C	B	C	A
<i>F</i> _{IS}		0.346	—0.040	0.231	—0.088	—0.109	0.487	1.000
<i>F</i> _{IT}		0.388	—0.003	0.273	0.132	—0.014	0.509	1.000
<i>F</i> _{ST}		0.063	0.036	0.054	0.202	0.086	0.044	0.063

* Allelic frequencies do not conform with expectations from Hardy-Weinberg equilibrium.

† Pooling rare alleles causes frequencies to conform to Hardy-Weinberg expectations.

cranial variables show statistically significant ($P < 0.05$) secondary sexual variation across all four of the samples tested, and all previous studies have shown that *R. megalotis* does not exhibit significant sexual dimorphism (Hooper, 1952; Jones and Mursaloglu, 1961; Fisler, 1965; Hoffmeister, 1986), the sexes were pooled with individuals of unknown sex.

Intraspecific Ontogenetic Variation. Seven of the 14 cranial characters exhibit significant ($P \leq 0.05$) differences among the character means of the five age classes tested (Table 3). Five of the seven measurements previously have been shown to vary ontogenetically in western harvest mice (LR, LN, BR, LP, and ZB); four of these are measurements of the rostral area (Hooper, 1952; Fisler, 1965). SNK mul-

Table 1. Continued.

Sample	n	SDH	α -GPD	ADH	Got-1	Got-2	NP	PGM
SCRUZI	20	—A	A (0.97) B (0.03)	—A	A	B	B	A
SCATI	15	—A (0.93)* —B (0.07)	A	—A	A	B	B	A
PTMUGU	20	—A	A (0.87) B (0.13)	—A (0.95) —B (0.05)	A (0.95) B (0.05)	B	B	A (0.97) B (0.03)
DELREY	15	—A	A (0.97) C (0.03)	—A	A	B	A (0.07) B (0.93)	A
ANAHAM	15	—A	A	—A	A	B (0.97) C (0.03)	B (0.97) C (0.03)	A
NEWPRT	11	—A	A	—A (0.96) —B (0.04)	A (0.96) B (0.04)	A (0.09) B (0.64) C (0.27)	B (0.91) C (0.09)	A
STYNEZ	18	—A (0.97) —B (0.03)	A	—A	A	B (0.97) C (0.03)	B	A (0.97) B (0.03)
NSBARB	14	—A	A	—A	A	B (0.86) C (0.14)	B	A
DEVERO	13	—A	A	—A	A	B (0.92) C (0.08)	A (0.08)* B (0.92)	A
GOLETA	13	—A	A	—A	A	B (0.96) C (0.04)	B (0.96) C (0.04)	A
CARPUP	12	—A	A	—A	A	B	B	A
CARPIN	14	—A	A (0.89) B (0.11)	—A	A	B (0.96) C (0.04)	B	A (0.96) C (0.04)
LACOU	11	—A	A	—A	A (0.96) B (0.04)	B (0.91) C (0.09)	B (0.96) C (0.04)	A
ORANGE	10	—A	A	—A (0.90)* —B (0.10)	A (0.95) B (0.05)	B	B	A
SDIEGO	7	—A	A	—A (0.93) —B (0.07)	A (0.93) B (0.07)	A (0.07) B (0.93)	B	A
F _{IS}		0.689	—0.110	0.325	—0.057	0.014	0.163	—0.031
F _{IT}		0.704	—0.018	0.363	—0.018	0.141	0.205	—0.004
F _{ST}		0.049	0.083	0.057	0.037	0.128	0.049	0.026

multiple-range tests record no consistent pattern of ontogenetic variation (Table 3). Although three variables (GL, LR, and ZB) exhibit significant variation in both samples tested, only ZB shows a similar pattern in both cases. Classes 2, 3, and 4 are statistically similar for two variables (LN and ZB) in the Santa Catalina Island sample and for five variables (GL, DBC, LR, ZB, and LP) in the Santa

Barbara County group (Table 3). In the former sample, BR is the only character for which age class 2 (subadult) was significantly different from all other age classes, and LR is the only character in which age classes 4 (adult) and 5 (including middle-aged and old adults) were significantly different from each other and from age classes 2 and 3. As there was no consistent pattern of ontogenetic variation ev-

Table 1. Continued.

Sample	n	6-PGD	G6PDH	Dia	ADA	Ck-2	Est-2	H	P (95%)	P (99%)
SCRUZI	20	C	B	B	A (0.20)* B (0.80)	—A	B (0.07)* C (0.93)	0.003	6.7	10.0
SCATI	15	C	B	B	A (0.60) B (0.40)	—A (0.87)* —B (0.13)	B (0.10) C (0.90)	0.044	20.0	23.3
PTMUGU	20	C	B	B	A (0.05) B (0.95)	—A	B (0.05) C (0.95)	0.038	20.0	26.7
DELREY	15	C	B	B	A (0.13) B (0.87)	—A	B (0.10) C (0.90)	0.031	13.3	16.7
ANAHM	15	C	B	B	A (0.20)* B (0.80)	—A	B (0.10) C (0.90)	0.038	20.0	26.7
NEWPRT	11	C	B	B	A (0.27) B (0.23) C (0.41) D (0.32)	—A	A (0.04) B (0.23) C (0.41) D (0.32)	0.076	16.7	23.3
STYNEZ	18	A (0.06) C (0.94)	B	B	B (0.89) D (0.11)	—A	B (0.33)* C (0.67)	0.054	13.3	30.0
NSBARB	14	C	B	B	B (0.93) D (0.07)	—A	B (0.39)* C (0.61)	0.036	10.0	10.0
DEVERO	13	C	B	A (0.08)* B (0.92)	B	—A	B (0.54) C (0.46)	0.044	16.7	23.3
GOLETA	13	C	A (0.04) B (0.96)	B	B (0.81) C (0.19)	—A	B (0.27) C (0.73)	0.049	13.3	26.7
CARPUP	12	C (0.96) D (0.04)	B	B	B	—A	A (0.04) B (0.25) C (0.67) D (0.04)	0.039	6.7	10.0
CARPIN	14	C	B	B	B (0.96) C (0.04)	—A	A (0.04) B (0.21) C (0.68) D (0.07)	0.040	10.0	23.3
LACOU	11	C	B	B	A (0.04) B (0.96)	—A	A (0.04) B (0.50) C (0.46)	0.036	13.3	23.3
ORANGE	10	C	B	B	B	—A	B (0.30) C (0.65) D (0.05)	0.027	13.3	13.3
SDIEGO	7	B (0.07) C (0.93)	B	B	A (0.21) B (0.79)	—A	B (0.50) C (0.50)	0.057	26.7	26.7
F _{IS}		−0.063	−0.040	1.000	0.275	1.000	−0.087			
F _{IT}		−0.008	−0.003	1.000	0.424	1.000	0.069			
F _{ST}		0.052	0.036	0.072	0.206	0.126	0.143			

ident, we regard specimens classed age 2 or above as adults and specimens classed ages 1 or 0 as juveniles. Subadults and adults were pooled for all subsequent analyses.

Results of our examination of ontogenetic variation in *R. megalotis* generally agree with those of Hooper (1952), Fisler (1965), and Hoffmeister (1986). Older mice, particularly those in age classes

5 and 6, are larger on average than animals classed ages 2–4 (Table 3). Hooper (1952) noted that senile individuals (age class 6) are unsatisfactory for use in taxonomic treatments because their skulls are often misshapen and their teeth are excessively eroded. Fisler (1965), therefore, decided to eliminate both old adults and juveniles from his study of geographic variation of harvest mice in the San

Table 2. Geographic variation in 11 cranial measurements (millimeters) for 17 populations of *Reithrodontomys megalotis* from southern California. Population samples and measurements are explained in the Appendix and Methods section. Vertical lines alongside each geographic sample indicate statistically homogeneous subsets derived from a Student-Newman-Keuls multiple range test. All *F*-statistics are significant (*P* < 0.0001).

Sample no.	n	Mean	Range	SD	CV
Greatest length of skull (GL) (<i>F</i> = 16.38)					
8	25	19.97	18.62–21.10	0.61	3.04
9	21	20.05	19.19–20.76	0.41	2.06
4	11	20.10	19.27–20.64	0.43	2.14
16	20	20.14	18.50–21.01	0.68	3.40
10	24	20.16	19.25–21.39	0.57	2.81
12	28	20.17	19.25–21.32	0.49	2.42
3	50	20.17	18.98–21.45	0.53	2.62
6	12	20.17	18.47–21.25	0.86	4.25
15	14	20.23	19.29–21.46	0.68	3.34
17	23	20.24	19.31–21.55	0.54	2.66
11	29	20.31	18.70–21.52	0.70	3.47
14	18	20.35	19.61–21.29	0.43	2.13
5	17	20.40	18.90–21.79	0.79	3.86
13	24	20.44	19.47–21.22	0.46	2.25
7	19	20.52	19.78–21.41	0.48	2.34
2	94	21.20	18.56–22.78	0.74	3.50
1	28	21.39	19.44–22.25	0.62	2.89
Depth of braincase (DBC) (<i>F</i> = 6.81)					
8	25	6.43	6.06–6.77	0.18	2.86
13	24	6.47	5.84–7.01	0.27	4.19
10	24	6.48	6.15–7.00	0.22	3.32
14	18	6.51	6.04–7.03	0.24	3.64
17	23	6.51	6.02–6.81	0.17	2.55
16	20	6.52	6.25–6.93	0.18	2.75
6	12	6.52	6.21–6.86	0.18	2.76
12	28	6.52	6.20–6.86	0.18	2.77
15	14	6.53	5.99–6.86	0.26	4.03
11	29	6.54	6.19–6.98	0.21	3.17
9	21	6.55	6.31–6.89	0.18	2.75
4	11	6.58	6.32–6.91	0.21	3.22
5	17	6.60	6.29–6.98	0.18	2.77
7	19	6.61	6.32–6.86	0.16	2.43
3	50	6.61	6.20–7.21	0.20	2.98
1	28	6.65	6.22–7.00	0.20	3.04
2	94	6.75	6.22–7.31	0.20	3.00
Intermeatus width (IW) (<i>F</i> = 2.77)					
10	24	2.28	2.10–2.50	0.12	5.06
9	21	2.30	2.10–2.70	0.12	5.40
4	11	2.31	2.10–2.50	0.15	6.26
8	25	2.32	2.00–2.70	0.17	7.34
15	14	2.33	2.10–2.60	0.13	5.69
11	29	2.37	2.10–2.80	0.20	8.60
13	24	2.37	2.20–2.60	0.13	5.30
17	23	2.38	2.20–2.80	0.14	5.94
7	19	2.38	2.00–3.00	0.22	9.30
12	28	2.40	2.00–2.70	0.15	6.27
16	20	2.40	1.90–3.00	0.23	9.65
3	50	2.40	1.51–2.90	0.23	9.57
14	18	2.41	2.20–2.80	0.16	6.61
1	28	2.43	1.54–2.90	0.24	9.90
2	94	2.44	1.10–2.90	0.24	9.72
6	12	2.47	2.30–2.60	0.10	3.99
5	17	2.57	2.20–2.80	0.17	6.42

Table 2. Continued.

Sample no.	n	Mean	Range	SD	CV
Length of rostrum (LR) ($F = 15.41$)					
15	14	6.24	5.60–6.80	0.32	5.10
10	24	6.26	5.60–6.70	0.25	3.91
4	11	6.27	5.90–6.80	0.28	4.46
16	20	6.28	5.50–6.90	0.37	5.86
3	50	6.30	5.50–6.90	0.33	5.27
9	21	6.31	5.70–6.70	0.23	3.68
8	25	6.34	5.80–6.90	0.28	4.39
13	24	6.38	5.80–6.80	0.23	3.60
6	12	6.40	5.70–7.10	0.44	6.79
5	17	6.41	5.70–7.10	0.39	6.01
12	28	6.41	5.60–7.20	0.37	5.74
11	29	6.42	5.60–7.10	0.40	6.16
7	19	6.47	5.80–7.10	0.30	4.67
17	23	6.47	6.10–7.30	0.32	4.94
14	18	6.74	6.20–7.50	0.33	4.88
2	94	6.86	5.50–7.60	0.39	5.68
1	28	7.04	5.60–7.80	0.43	6.05
Length of braincase (LBC) ($F = 20.07$)					
9	21	13.80	13.28–14.16	0.26	1.88
16	20	13.85	12.86–14.54	0.44	3.19
6	12	13.89	12.89–14.66	0.54	3.89
17	23	13.90	13.25–14.73	0.37	2.63
10	24	13.92	13.28–14.59	0.40	2.91
11	29	14.03	12.92–14.84	0.46	3.26
5	17	14.10	13.33–15.09	0.48	3.37
8	25	14.13	12.76–15.05	0.62	4.41
7	19	14.23	13.62–15.19	0.40	2.82
3	50	14.44	13.37–15.69	0.53	3.64
14	18	14.48	13.95–15.16	0.36	2.47
13	24	14.49	13.50–15.35	0.40	2.73
4	11	14.53	13.30–15.19	0.61	4.17
12	28	14.63	13.69–15.23	0.37	2.56
1	28	14.88	14.04–15.44	0.37	2.46
15	14	14.90	14.48–15.79	0.37	2.51
2	94	14.96	13.39–16.26	0.62	4.17
Length of nasals (LN) ($F = 20.08$)					
15	14	7.25	6.60–8.30	0.47	6.40
16	20	7.29	6.40–8.10	0.45	6.20
9	21	7.41	6.50–8.10	0.39	5.26
8	25	7.50	6.60–8.60	0.42	5.64
10	24	7.51	6.90–7.80	0.29	3.81
3	50	7.53	6.80–8.40	0.38	5.07
17	23	7.56	6.60–8.50	0.51	6.69
6	12	7.58	6.60–8.40	0.53	7.03
5	17	7.60	6.40–8.60	0.56	7.37
11	29	7.64	6.30–8.60	0.52	6.78
7	19	7.74	6.60–8.90	0.55	7.08
13	24	7.75	7.00–8.60	0.43	5.56
12	28	7.75	7.00–8.60	0.41	5.27
4	11	7.76	7.00–8.30	0.38	4.86
14	18	7.97	7.20–8.80	0.42	5.32
2	94	8.25	6.90–9.50	0.51	6.13
1	28	8.59	6.90–9.40	0.57	6.61

Table 2. Continued.

Sample no.	n	Mean	Range	SD	CV
Length of incisive foramen (LIF) ($F = 14.52$)					
15	14	4.24	3.80-4.60	0.23	5.53
4	11	4.25	3.90-4.50	0.19	4.51
9	21	4.25	4.00-4.60	0.15	3.61
3	50	4.31	4.00-4.70	0.16	3.80
8	25	4.32	3.90-4.70	0.20	4.68
10	24	4.32	4.10-4.70	0.18	4.05
17	23	4.33	4.00-4.60	0.19	4.27
5	17	4.34	3.80-4.70	0.24	5.53
16	20	4.35	4.00-4.60	0.17	3.99
11	29	4.35	3.80-4.80	0.20	4.58
6	12	4.36	3.80-4.80	0.28	6.45
7	19	4.37	4.00-4.70	0.20	4.52
12	28	4.37	4.10-4.60	0.16	3.62
13	24	4.38	4.10-4.70	0.16	3.54
14	18	4.48	4.00-4.80	0.19	4.23
2	94	4.63	4.00-5.00	0.22	4.69
1	28	4.66	4.30-5.00	0.21	4.47
Zygomatic breadth (ZB) ($F = 29.31$)					
6	12	10.12	9.33-10.76	0.35	3.42
4	11	10.13	9.79-10.67	0.28	2.75
17	23	10.14	9.59-10.55	0.28	2.78
8	25	10.17	9.54-10.66	0.32	3.16
10	24	10.18	9.65-10.65	0.24	2.39
16	20	10.19	9.63-10.93	0.34	3.37
9	21	10.19	9.79-10.64	0.23	2.28
12	28	10.23	9.71-10.86	0.28	2.76
3	50	10.26	9.78-10.98	0.30	2.88
11	29	10.27	9.17-10.99	0.39	3.77
7	19	10.30	9.84-10.85	0.29	2.83
15	14	10.31	9.89-10.99	0.27	2.65
14	18	10.34	9.66-11.18	0.33	3.21
13	24	10.38	10.01-11.10	0.29	2.80
5	17	10.50	9.76-11.27	0.43	4.09
1	28	10.90	10.19-11.40	0.29	2.69
2	94	10.97	9.99-11.96	0.34	3.07
Length of molar tooth row (AL) ($F = 18.58$)					
10	24	3.11	2.80-3.40	0.14	4.48
15	14	3.11	3.00-3.40	0.14	4.34
9	21	3.12	3.00-3.30	0.09	2.85
11	29	3.13	2.80-3.40	0.14	4.36
3	50	3.14	2.90-3.40	0.12	3.92
4	11	3.15	3.00-3.40	0.13	4.11
8	25	3.16	3.00-3.30	0.10	3.27
12	28	3.17	2.90-3.40	0.13	4.10
17	23	3.17	3.00-3.50	0.11	3.58
6	12	3.18	3.10-3.30	0.08	2.37
13	24	3.19	3.00-3.50	0.14	4.33
7	19	3.19	3.00-3.40	0.10	3.04
5	17	3.22	3.00-3.40	0.11	3.34
14	18	3.23	3.00-3.40	0.13	4.11
16	20	3.28	3.00-3.50	0.12	3.69
2	94	3.36	3.10-3.80	0.11	3.36
1	28	3.40	3.00-3.60	0.14	4.12

Table 2. Continued.

Sample no.	n	Mean	Range	SD	CV
Breadth of rostrum (BR) ($F = 9.08$)					
15	14	3.00	2.77–3.48	0.19	6.44
8	25	3.18	2.89–3.51	0.18	5.51
12	28	3.19	2.92–3.39	0.12	3.85
3	50	3.20	2.85–4.16	0.23	7.21
17	23	3.25	2.92–3.51	0.14	4.42
9	21	3.25	2.89–3.51	0.17	5.14
4	11	3.27	3.06–3.53	0.14	4.36
14	18	3.28	3.04–3.65	0.19	5.77
7	19	3.28	3.02–3.44	0.11	3.36
11	29	3.29	3.07–3.70	0.14	4.23
16	20	3.29	3.07–3.49	0.12	3.64
13	24	3.30	2.89–3.62	0.17	5.10
10	24	3.31	2.99–3.51	0.14	4.12
6	12	3.32	3.11–3.61	0.14	4.29
5	17	3.39	3.05–3.82	0.20	6.01
1	28	3.41	2.40–3.88	0.25	7.21
2	94	3.43	3.13–3.90	0.18	5.32
Length of palate (LP) ($F = 17.91$)					
10	24	7.82	7.10–8.50	0.36	4.63
9	21	7.84	7.50–8.20	0.22	2.81
4	11	7.88	7.70–8.00	0.12	1.48
12	28	7.89	6.50–8.60	0.39	4.96
15	14	7.89	7.50–8.30	0.27	3.39
6	12	7.92	7.40–8.50	0.31	3.92
3	50	7.93	7.50–8.50	0.25	3.21
8	25	7.93	7.10–8.60	0.30	3.80
11	29	7.93	7.30–8.60	0.33	4.10
17	23	7.96	7.50–8.70	0.28	3.51
16	20	8.00	7.30–8.50	0.33	4.10
13	24	8.05	7.70–8.50	0.23	2.84
5	17	8.05	7.30–8.90	0.40	4.95
7	19	8.14	7.00–8.50	0.34	4.20
14	18	8.18	7.70–8.80	0.32	3.87
2	94	8.44	7.50–9.10	0.32	3.76
1	28	8.58	7.70–9.20	0.34	3.91

Francisco Bay area. The majority of mice in this study fall into age classes 2, 3, and 4. We decided to include animals of age class 6 in the samples used in the final taxonomic analyses because they do not consistently differ significantly from younger animals, and only a few individuals of this age class occur in any one sample.

Geographic Variation

Analysis of variance (ANOVA) detected statistically significant ($P < 0.0003$) differences among the 17 samples for all 11 characters (Table 2), thus invalidating the null hypothesis of no statistically significant geographic variation among populations. Because all characters show significant interpopulation heterogeneity, it is appropriate to use them in further multivariate procedures. The greatest interlocality variation (F -ratios > 14) occurs in ZB,

LN, LBC, AL, LP, GL, and LR; whereas IW, DBC, and BR exhibit the least variation (F -ratios < 10 ; Table 2). Western harvest mice from Santa Catalina and Santa Cruz islands average larger than specimens from other localities in 9 of 11 variables (81.8%); mice from Goleta and Devereux sloughs, Playa Del Rey, and San Clemente Island average smaller than other populations for 5–7 of 11 characters (45.5–63.6%) (Table 2). Multivariate analysis of variance (MANOVA) revealed that statistically significant differences (F transformation of Wilk's lambda statistic = 5.87; d.f. = 176, 3946; $P < 0.0001$) exist among the 17 samples. Therefore, it is appropriate to investigate the dispersion of these samples within discriminant space.

The mean centroids for each of the 17 samples are plotted on the first three canonical variate axes (Fig. 5). Circles representing 95% confidence limits (Pimentel and Smith, 1986b) are drawn around each

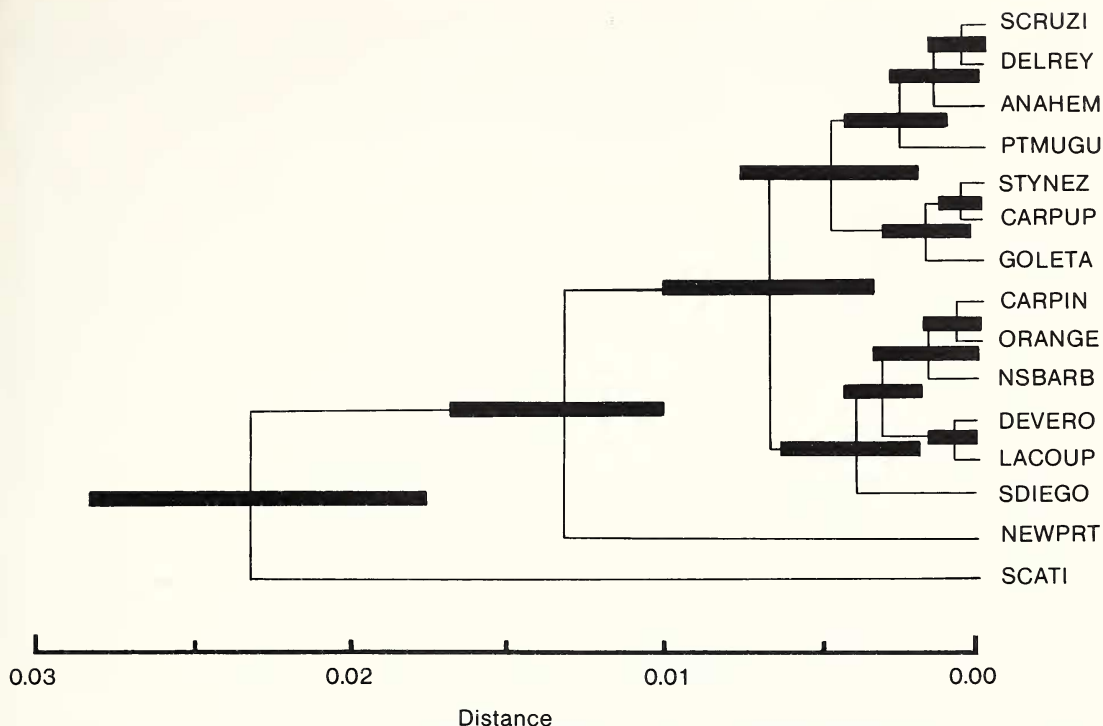


Figure 3. UPGMA phenogram constructed from Nei's distance values. Bars denote standard errors of the branch lengths.

centroid. The variance-covariance matrix yielded 11 canonical variates from among the 11 cranial characters used for all 17 samples. Only the first six canonical variates exhibit statistically significant (χ^2 , $P < 0.017$) morphological variation. The first three axes account for a combined total of 84.6% of the

total phenetic variation (Table 4). Although canonical variates 4–6 are also significant ($P \leq 0.02$), each provides little additional discrimination between the localities; axes 7–11 account for less than 5% of the total between-group variation. Therefore, there is little distortion of the phenetic distances between

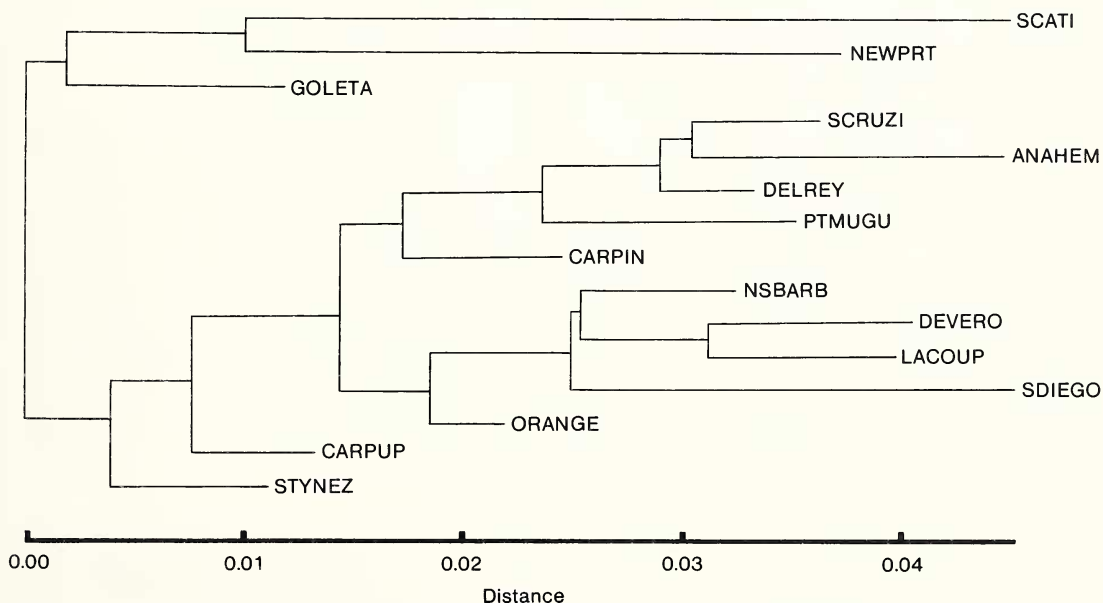


Figure 4. Distance-Wagner tree based on Rogers' distance values and rooted at the midpoint.

Table 3. Cranial variables in *Reithrodontomys megalotis* from southern California that exhibit significant ontogenetic variation. Statistically homogeneous subsets are derived from the Student-Newman-Keuls multiple range test and are shown by lines below the means for each age category. Any age categories underlined together are not significantly different ($P > 0.05$) from one another. Character acronyms are described in the Methods section. Age classes 0 and 1 were dropped prior to analysis because of insufficient sample size. Age classes 5 and 6 are combined.

Character	Age class				F-ratio	Probability
	2	3	4	5		
Santa Catalina Island (sample 2, n = 93)						
GL	<u>20.82</u>	<u>21.06</u>	<u>21.65</u>	<u>22.06</u>	12.48	0.000
LR	<u>6.76</u>	<u>6.77</u>	<u>7.02</u>	<u>7.30</u>	7.51	0.000
LN	<u>8.30</u>	<u>8.18</u>	<u>8.55</u>	<u>8.82</u>	5.83	0.001
ZB	<u>10.87</u>	<u>10.92</u>	<u>11.09</u>	<u>11.22</u>	3.82	0.013
BR	<u>3.30</u>	<u>3.47</u>	<u>3.50</u>	<u>3.48</u>	7.66	0.000
n	27	38	19	9		
Santa Barbara County (samples 8 and 11, n = 51)						
GL	<u>19.76</u>	<u>20.09</u>	<u>20.20</u>	<u>20.82</u>	4.95	0.005
DBC	<u>6.54</u>	<u>6.42</u>	<u>6.44</u>	<u>6.67</u>	4.42	0.008
LR	<u>6.19</u>	<u>6.37</u>	<u>6.48</u>	<u>6.63</u>	3.04	0.038
ZB	<u>10.02</u>	<u>10.20</u>	<u>10.35</u>	<u>10.52</u>	3.99	0.013
LP	<u>7.77</u>	<u>7.92</u>	<u>8.06</u>	<u>8.16</u>	3.11	0.035
n	10	27	5	9		

populations if the character space is reduced from 11 dimensions to only three.

The contributions of individual characters to the separation of centroids are depicted in Figure 5 by the magnitude and direction of the character vectors. With the exception of GL and IW, the remaining variables load positively on the first axis (Table 4, Fig. 5), suggesting that this represents a size axis. There were only a few variables that contributed a significant proportion of their variance to subsequent axes (Table 4, Fig. 5). Characters with more than 50% of their variance explained on the first axis were ZB, AL, DBC, and LN (Table 4). The only character on the second axis to have more than 50% of its variance explained is LBC (98%), whereas GL, LIF, and LP each contribute more than 35% of their variance to the second axis. On the third axis only LR had more than 50% of its variance explained, whereas IW had about 30% of its variance explained. On the remaining axes there were no characters with more than 40% of their variance explained.

Considerable phenetic overlap of the populations is evident in the plots of the first three canonical variates (Fig. 5). The overlapping confidence circles suggest that there is little significant variation among

the southern California harvest mouse populations and that only small-scale differentiation is occurring. Canonical variate 1, which reflects overall size, accounts for 53.7% of the variation. Two of the island localities (Santa Cruz and Santa Catalina islands) have animals divergent in size (CV-1 in Fig. 5), but not in shape (CV-2 and CV-3 in Fig. 5), from those in adjacent mainland localities; this is consistent with the results of the SNK multiple-range tests (Table 2). When the first axis is eliminated by plotting the second against the third (Fig. 5B), the two island samples are indistinguishable from the remaining mainland samples. Thus, despite the magnitude of size differences exhibited by these two island samples, both populations still maintain the same basic skull shape as do mainland populations. There are no other distinct groupings of population samples in Figure 5 that are consistent with geography or with currently accepted taxonomy. Samples from the salt marshes of southern California (samples 3–6) currently allocated to *R. m. limicola* are indistinguishable on both the size (CV-1 in Fig. 5) and shape (CV-2 and 3 in Fig. 5) axes from other southern California harvest mouse populations (samples 7–17).

The degree of phenetic overlap of the 17 samples

Figure 5. Discriminant function plots of the first three canonical vectors. Circles represent 95% confidence limits about the mean centroid. Numbers refer to samples described in Figure 1 and in the Appendix. Contributions of individual characters to the separation of locality centroids are indicated by the magnitude and direction of the character vectors. For clarity, only the largest vectors are depicted.

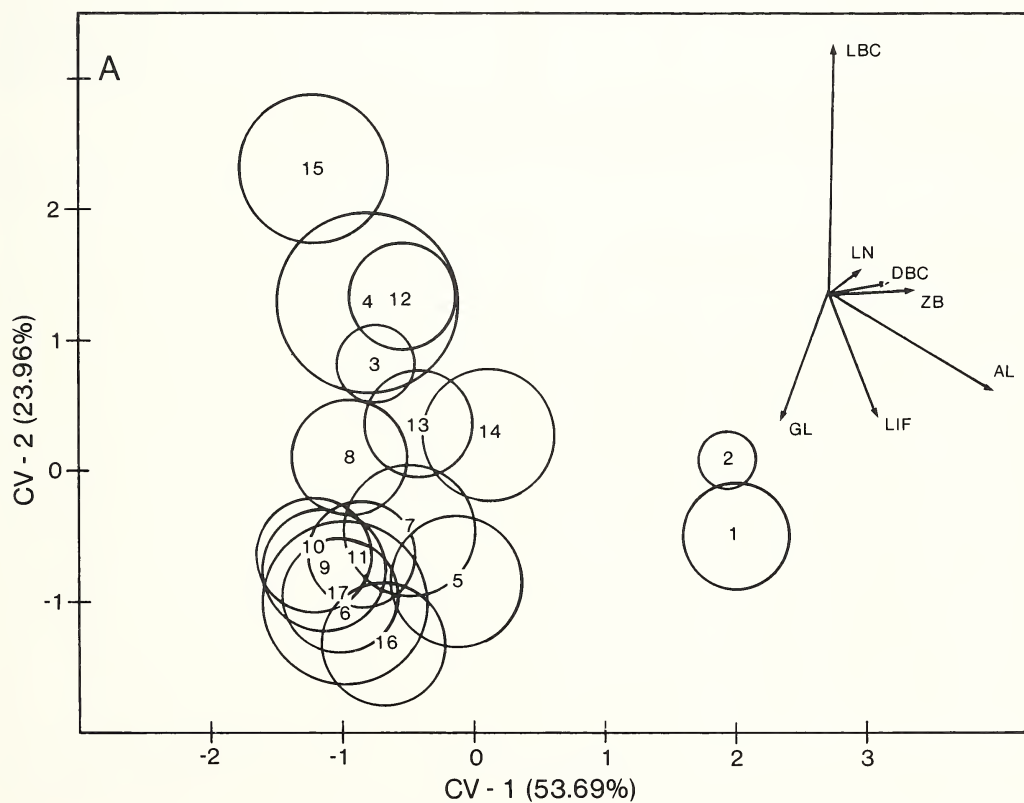
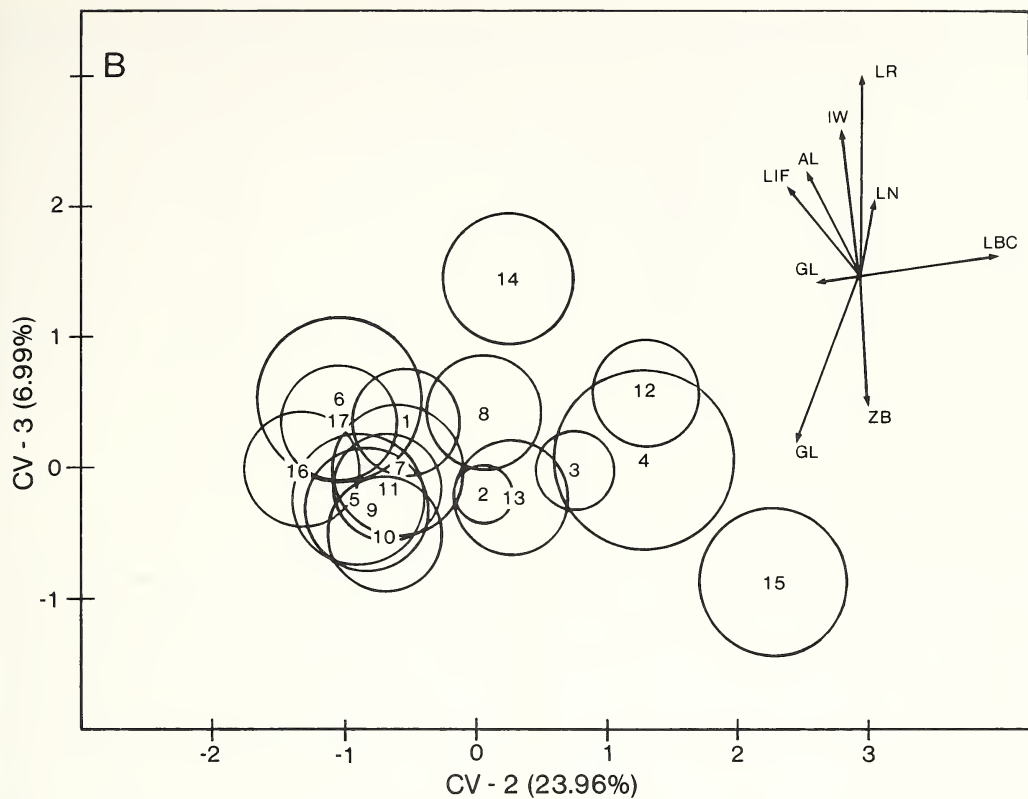


Table 4. Character loadings and percent of overall morphological variance explained for the first six canonical vectors of interlocality phenetic variation in *Reithrodontomys megalotis* from southern California.

Character	Canonical variates					
	1	2	3	4	5	6
GL	-0.215	-0.348	-0.467	0.005	0.179	-0.233
DBC	0.294	0.036	-0.082	-0.111	-0.205	0.450
IW	-0.062	-0.079	0.386	0.219	-0.633	-0.140
LR	0.066	0.038	0.544	0.143	0.210	0.500
LBC	0.050	0.760	0.050	-0.014	-0.110	-0.055
LN	0.158	0.086	0.192	-0.335	0.020	-0.177
LIF	0.215	-0.355	0.240	-0.108	-0.300	0.323
ZB	0.416	0.026	-0.356	0.068	0.081	0.303
AL	0.762	-0.271	0.277	0.674	-0.198	-0.420
BR	0.138	-0.188	-0.025	-0.511	-0.573	-0.121
LP	0.111	-0.221	0.170	0.275	0.061	-0.227
Percent	53.69	23.96	6.99	4.98	3.06	2.39

was further assessed by comparing the proportion of individuals from each locality that was misclassified by the discriminant function analysis. Of 457 specimens, a total of 171 (37%) were classified correctly to their *a priori* designated samples by the classification procedure of the discriminant function analysis (Table 5). The degree of morphological overlap among mainland and island locality samples in southern California is evident in the percentage of misclassified individuals, which averaged 63%. The most distinctive locality samples were from SCLEMI (14% misclassified), SCRUIZ and LACUP (39% misclassified each), and DELREY and SCATI (45% misclassified each), whereas the least distinctive locality samples were NSBARB and

SSBARB (localities 8 and 11), which had 96% and 90% of their specimens misclassified, respectively. Of the 11 Santa Cruz Island specimens that were misclassified, five were classified with Santa Catalina Island (sample 2), three with the Los Angeles County upland site (sample 14), and one each with San Clemente Island (sample 15) and Orange County upland (sample 16). Of the 42 Santa Catalina Island specimens that were misclassified, 20 (48%) were classified with Santa Cruz Island whereas 16 (38%) were classified with Los Angeles and Orange County mainland localities (samples 4, 5, 14, and 16). Only two of the 14 San Clemente Island specimens were misclassified, one with the Goleta Slough sample (sample 10) and one with the Carpinteria upland

Table 5. Geisser classification of individual western harvest mice from southern California (n = 457). Rows are actual groups and columns are predicted groups. See Appendix for explanation of sample acronyms.

Actual locality	n	Percent classified correctly	Predicted locality				
			1	2	3	4	5
SCRUIZ	1	28	61	17	5		
SCATI	2	94	55	20	52	1	9
PTMUGU	3	50	6		3	7	6
DELREY	4	11	55			6	
ANAHM	5	17	41	2			7
NEWPR	6	12	25		1		
STYNEZ	7	19	42	1	1	1	
NSBARB	8	25	4		3		1
DEVERO	9	21	38				1
GOLETA	10	24	33				
SSBARB	11	29	10	2		2	2
CARPUP	12	28	50		1	1	5
CARPIN	13	24	21		1	1	2
LACUP	14	18	61	1	1		2
SCLEMI	15	14	86				
ORANGE	16	20	50		1		2
SDIEGO	17	23	13				

sample (sample 12). Of the 136 island specimens, 29 (21%) were misclassified with mainland localities, whereas 25 (7.8%) of the 321 mainland specimens were misclassified with island localities. Specimens of *R. m. limicola* (samples 3–6) do not show a consistent pattern of misclassification. Of the 72 specimens misclassified in these four localities, only 17 (24%) were misclassified with other *R. m. limicola* populations (Table 5). Thus, the low proportions of correctly classified individuals in this discriminant function analysis suggest that the degree of phenetic overlap among the samples is great and that there are only gradual phenetic changes occurring among the 17 southern California samples.

DISCUSSION

GENETIC VARIABILITY

Population variation (F_{ST}) of 8.1% among the 15 populations of *R. megalotis* is indicative of low to moderate variation in mammals (Wright, 1978; Hartl, 1988). This value is comparable to that found among western populations of *Peromyscus maniculatus* (Calhoun *et al.*, 1988) but lower than that value calculated for populations across the range of *P. maniculatus* (Avisé *et al.*, 1979). Our F_{ST} is similar to the value calculated for populations of *Cynomys mexicanus* (McCullough and Chesser, 1987) and for populations of *C. ludovicianus* within geographically separated regions (Chesser, 1983). The inbreeding coefficients ($F_{IS} = 0.245$, $F_{IT} = 0.307$) are rather high; this might be explained by the fact that of the 93 cases where a population is heterozygous for a particular locus, 14 of these do not

conform to Hardy-Weinberg equilibrium (Table 1). In most of these 14 cases there is the occurrence of a “rare” allele in the homozygous state or in heterozygosity with another rare allele.

From the F_{ST} value, one can calculate the number of dispersers among populations, assuming genetic drift and dispersal are in equilibrium (Wright, 1969). The result is 2.84 individual dispersers per generation among the 15 populations of *R. megalotis* examined. This is comparable to values found in other rodents (McCullough and Chesser, 1987; Calhoun *et al.*, 1988). With the exception of the island populations, *R. megalotis* probably was distributed continuously throughout southern California prior to the urbanization of the last 100 years. This distribution would account for the high estimated rate of dispersal among populations, in spite of the great distance between sample sites.

Average heterozygosity has not been characterized from allozyme data for any species of *Reithrodontomys* until now (Arnold *et al.*, 1983; Nelson *et al.*, 1984), but the heterozygosity levels we detected in southern California populations of *R. megalotis* fall within levels calculated for *Peromyscus* species in California (Avisé *et al.*, 1974, 1979; Smith, 1979; Gill, 1980; Calhoun *et al.*, 1988) and elsewhere in North America (Selander *et al.*, 1971; Smith *et al.*, 1973; Kilpatrick and Zimmerman, 1975), with the exception of the population from Santa Cruz Island. Insular populations of mammals have, on the average, 42% less genetic variability (measured by heterozygosity) than mainland populations of the same species (Kilpatrick, 1981). The average heterozygosity across all mainland samples examined herein is 0.043, whereas

Table 5. Continued.

Predicted locality												
6	7	8	9	10	11	12	13	14	15	16	17	
	1							3	1	1		
	2			1	1		1	4		2	1	
	2	1	3	3	1	11	1	1	8	2	1	
						2			1	2		
3	1	1								3		
3			1		1			1		2	2	
2	8		2	1	1					2		
1	1	1	2	2		4	2	1	1	2	4	
	1		8	5	3					2	1	
	3		5	8	2		3			1	2	
2	2	2	4	6	3			1		2	1	
		1		2		14		2	1		1	
	3			4	1	6			1			
1				1				11	1			
				1		1			12			
	1	1	3				1			10	1	
7	2		4		3					4	3	

heterozygosity of the Santa Cruz Island sample is only 0.003. This primarily is the result of an increase in the number of monomorphic loci and the absence of most rare and low-frequency alleles found on the mainland and may be interpreted as the result of founder effect (Kilpatrick, 1981; Berry, 1986). This phenomenon is not evident in the sample from Santa Catalina Island ($H = 0.044$; $P = 20\%$). The effect of genetic drift appears to have a strong influence on this population, however, as seen in the predominance of alternate alleles for two loci (Pep-D^B and ADA^A).

Neither the cluster analysis nor the distance-Wagner analysis provides results concordant with geographic or ecological patterns. There are no evident north-south clinal trends, nor are there any wetland-upland patterns of clustering. The distance and similarity data do not support the recognition of a subspecies limited to coastal salt marshes, nor do they support the recognition of a unique subspecies on Santa Cruz Island (Nei's I of 0.999 with the sample from DELREY). The Santa Catalina Island sample has the lowest identity value (0.977) with other samples of harvest mice (Fig. 3), but again, this is very high for a population that has been classified as a distinct subspecies.

Standard errors of the branch lengths of the UPGMA dendrogram overlap below the 0.01 level, suggesting that the branch points below the 0.01 level are not reliable (Fig. 3; Nei *et al.*, 1985). The standard error of the branch points for the samples from Newport Bay and Santa Catalina Island nearly overlap and must be considered with caution. The possibility exists that a UPGMA tree calculated from electrophoretic data can deviate greatly from the true evolutionary tree. As the number of loci examined increases, the likelihood that the UPGMA tree deviates from the true tree decreases (Nei *et al.*, 1983). Having considered 30 loci, we are confident that our tree is a reasonable representation of the relationships among the populations. Therefore, we conclude that the distance values among the populations we examined are so low that they reflect extremely close relationship and little genetic divergence in western harvest mice in southern California.

MORPHOLOGIC VARIATION

Canonical variate analysis of the morphologic data reveals that, aside from the two island populations, there is little geographic variation in overall cranial morphology among southern California populations of *R. megalotis*. There is a high degree of phenetic overlap among the 17 samples with no clear associations evident among size, geography, ecology, or currently accepted taxonomy. This is best exemplified by the low proportions (37%) of correctly classified individuals in the discriminant function analysis and in the extent to which the 17 localities overlap in multivariate space (Fig. 5). These data suggest that only gradual small-scale phenetic

changes have taken place within *R. megalotis* populations in this region. This pattern of morphologic variation is probably attributable, at least in part, to the absence of any major geographic barriers in the region that would result in morphologic divergence.

Analysis of cranial characters indicates some separation (size only) of the Santa Cruz and Santa Catalina island populations from other samples. As there are no distinct shape differences, these populations may have been isolated from parental populations of *R. megalotis* fairly recently. Misclassifications of Santa Cruz and Santa Catalina island individuals (Table 5) tend to be to the other island, rather than to mainland or San Clemente Island samples. These data, when viewed in concert with the degree of phenetic overlap observed between the Santa Cruz and Santa Catalina island populations (Fig. 5), suggest that either gene flow has occurred between these two islands, or parallel (or convergent) evolution has occurred.

Island populations tend to be subject to strong directional selection because of their isolation and reduced gene flow with the mainland. Grant (1979b) suggested that the reduction in phenotypic variation in isolated populations is due both to a reduction in gene flow and to differentiation that results from random genetic drift and directional selection. By identifying characters or suites of characters that exhibit reduced variability, Zink (1986) suggested that it may be possible to identify important fitness traits. Also, by examining intraspecific morphological variation, it may be possible to determine whether any discrete, morphologically uniform samples exist that correspond to evolutionary units that may warrant subspecific classification (Cracraft, 1983; Zink, 1986).

All of the coefficients of variation (CVs) for cranial characters used in this study (Table 2) are less than 10%. In general, intermeatus width (IW) and characters of the rostrum (LN, LR, and BR) tend to be more variable than the other cranial characters (Table 2), whereas levels of variability are lower and fairly uniform among localities for greatest length of skull (GL), depth of brain case (DBC), and zygomatic breadth (ZB). The higher CVs obtained for IW, LN, LR, and BR could be indicative of inherent variation present in the populations studied or could be a result of higher than average measurement error with these four characters.

Two of the island samples (Santa Cruz and Santa Catalina islands) exhibit slightly higher levels of variability (mean CVs, 4.85 and 4.76, respectively) than the other island (San Clemente Island; mean CV, 4.49) and most of the mainland populations (mean CVs, 3.43–4.56). This contrasts with results obtained by Aquadro and Kilpatrick (1981) for *Peromyscus* on islands off the coast of Maine. Based on mean CV, the San Clemente Island sample did not show a consistent departure in variability from the mainland samples. There are no other consistent patterns of variation in mean CVs for cranial

characters that might correspond to ecological, environmental, or geographic parameters. Further, there are no clines evident in the CVs for cranial characters used in this study.

A number of studies have correlated morphological variability with niche breadth (Van Valen, 1965; Rothstein, 1973; Grant, 1979a; Power, 1983; Schnell *et al.*, 1986) or with changes in interspecific competition (Schoener, 1970). Deer mice occur sympatrically with harvest mice in very low densities on the mainland but are abundant on the California Channel Islands. It is possible that the increased density of deer mice caused harvest mice on Santa Cruz and Santa Catalina islands to shift their niche and exploit a wider variety of foods. The slight increase in morphological variability and the increase in overall size observed in these island populations may be related to this increase in niche width.

Gigantism, accompanied by an increase in morphological variability, is a common phenomenon seen in small mammal species on islands, particularly in cricetid rodents (Foster, 1964; Lomolino, 1985). Lomolino (1985) explains this as the result of competitive release, which has an increasing effect as the size of the species decreases. Mainland populations of harvest mice in southern California are sympatric with many rodent species (depending on the locality), including sciurids, heteromyids, cricetids, and arvicolids, whereas island populations are sympatric with only two species, *Spermophilus beecheyi* (on Santa Catalina Island only) and *Peromyscus maniculatus*. This, too, may be a contributing factor to the increase in size observed in harvest mouse populations on Santa Cruz and Santa Catalina islands.

COVARIATION OF MORPHOLOGICAL AND PROTEIN CHARACTER SETS

Mayr (1963) suggested that natural selection acts on the total genotype through the phenotype rather than on individual genes or phenetic characters. However, Schnell and Selander (1981) suggested that protein and morphologic characters evolve independently because they are subject to different types of evolutionary pressures. The exact relationships between phenotypic and genotypic changes still are not well understood. Specifically, we know little about the heritability of observed patterns of morphometric size and shape variation (Atchley *et al.*, 1981), and we do not know the role that genetic variability plays in the structuring of phenotypic variability. Without data on the heritability and number of loci that contribute genetic variance to a particular morphological trait, it is impossible to determine whether allozymes and morphologies evolve independently (Zink, 1986). What is known is that most morphological traits are polygenic (controlled by many structural and regulatory genes) (Lewontin, 1974) and that the majority of genes are pleiotropic (affecting many different characters of

the phenotype) (Wright, 1980). Thus, the genotype and the phenotype are intimately intertwined systems that are composed of interacting components (Cheverud, 1982).

Racial affinities within a taxon can be examined in a number of ways, using biochemical, cytological, and phenetic data. However, analyses based on one data set, either phenetic or genetic, can give patterns of divergence or rates of change between populations that are different from those obtained from a comparative analysis of more than one type of variation. For example, Berry and Peters (1976), Pizzimenti (1976), Shvarts (1977), Schnell *et al.* (1978), Gill (1980), and Aquadro and Kilpatrick (1981) all failed to find concordance between electrophoretic variability and detectable levels of morphological or karyotypic variation. Selection may be operating in diverse ways at different levels (Schnell and Selander, 1981). There are, however, an increasing number of geographic variation studies on mammals that have found concordant patterns of relationships, based on biochemical, cytological, and morphological analyses (e.g., *Rattus*—Patton *et al.*, 1975; *Dipodomys*—Best, 1983; Best *et al.*, 1986; *Eutamias*—Sullivan, 1985; *Thomomys*—Smith and Patton, 1988). These studies have shown that operationally independent estimates of divergence may accurately reflect similar trends in genomic variability and phylogenetic relationships within a taxon.

In our study of western harvest mice from southern California, the results of the electrophoretic analyses generally were similar to the observed patterns of geographic variation delineated by the morphometric analyses. Both the genetic and the morphometric analyses demonstrate little geographic variation. Most populations cluster in no discernable geographic or taxonomic pattern. Samples from Santa Cruz and Santa Catalina islands were divergent in size from the other samples. The most divergent sample (Santa Catalina Island) also exhibited the greatest amount of genetic differentiation. The nature of this divergence can be explained by a nonclinal pattern of genic variation that is caused by the presence of uniquely fixed alleles and frequency differences at two loci. The absence of any significant genetic variation in the *R. megalotis* populations of southern California is probably a result of the absence of any major geographic barriers between populations in the region.

HYPOTHESES ON ISLAND COLONIZATION

Questions persist regarding how and when harvest mice colonized the islands. Von Bloeker (1967) suggested that harvest mice were accidentally introduced to San Clemente Island in bales of hay during this century. Such a recent colonization would not provide the population enough time to adapt to local conditions, and in fact, the sample we examined demonstrated no substantial morphological

divergence from the mainland populations. Conversely, the San Clemente Island sample had the highest percentage of correct Geisser classification (86%) of any sample included in this study (Pimentel and Smith, 1986b). This might be argued as evidence for some period of isolation and subsequent morphological differentiation, or it might be used as support for the founder effect. The fact that this species has only been collected from a small area on the island suggests that the latter case may be true; the population has not been on the island long enough to become well established and to have diverged from mainland populations but is still under the constraints of a founder effect and has low intrapopulation variability. Additional work on this population, including examination of allozymic variability, may shed some light on this question.

Harvest mouse populations on Santa Cruz and Santa Catalina islands show slight divergence from the mainland populations, the former only in cranial size and the latter in both cranial size and gene frequency at two loci. These data suggest a longer period of isolation (*i.e.*, perhaps since the last glacial episode, *ca.* 13,000 years BP) for these two islands than for the San Clemente Island population. Genetic interchange between the islands via Indian transport has been used to explain patterns of morphological variation in *Urocyon littoralis* (Collins, *in press*) and *P. maniculatus* (Gill, 1980). We do not feel that such a scenario is true for *R. megalotis* because of the low relative genic similarity of the samples, the extremely high similarity of the Santa Cruz Island sample to the coastal samples, and the lack of unique or rare alleles shared by the two island samples.

The question of when the islands were colonized by *R. megalotis* remains. Size divergence in two of the island samples suggests that western harvest mice were probably established on these islands prior to the last 100 years. Certainly Santa Catalina Island was colonized prior to the colonization of Santa Cruz Island. Besides the genetic evidence, there are ecological data to support this claim. Western harvest mice are far more abundant and widespread and are equally as common as *P. maniculatus* on Santa Catalina Island (Williams, 1986), whereas on Santa Cruz Island, harvest mice are limited to Prisoners' Harbor and the east end of the island and are caught in lower numbers (Bills, 1969; Williams, 1986).

Determining the time of colonization of the islands is extremely difficult. Geologic data do not support the existence of any land bridges between the mainland and any island, between northern and southern islands, or between any of the southern islands during the Pleistocene (Junger and Johnson, 1980; Vedder and Howell, 1980; Johnson, 1983). The Northern Channel Islands (Anacapa, Santa Cruz, Santa Rosa, and San Miguel) were connected as one superisland (Santarosae) several times during glacial episodes in the Pleistocene (Johnson, 1978). Santarosae reached its maximum size about 18,000 years

BP when sea level was approximately 120 m below its present-day level. With the end of full glacial conditions, sea level began to rise. Anacapa Island separated from Santarosae first about 12,000 years BP, followed by Santa Cruz Island at 11,500 years BP, and finally by San Miguel Island at 9,500 years BP (Johnson, 1978).

Several lines of evidence refute a pre-Holocene colonization of Santa Cruz Island by *R. megalotis*. Although the mammalian fossil record from Anacapa, San Miguel, and Santa Rosa islands has been well documented, there are no known fossils of harvest mice from these islands (D.A. Guthrie, *in litt.*; Lipps, 1964; White, 1966; Walker, 1980). Santa Cruz Island has a poor fossil record, but because it was connected by a land bridge to Anacapa prior to 12,000 years BP and to Santa Rosa and San Miguel islands prior to 11,500 years BP, we would predict that *R. megalotis* would have been detected in those islands' fossil record if the species had then been present on Santarosae. Therefore, it is probable that harvest mice reached Santa Cruz Island since it last separated from the Santarosae Island mass. Although the high standard errors on the genic data preclude setting divergence times to the branch points of the islands (Nei, 1972; Nei *et al.*, 1985; Sarich, 1977), Santa Cruz Island allozymically is indistinguishable from the mainland. This also supports a recent, probably late Holocene, colonization.

Setting a time for the colonization of Santa Catalina Island by harvest mice is more problematic. This population shows some genetic distinctiveness, although the genetic distance from the mainland is still less than 2.3%. Genetic distance between mainland and Santa Catalina Island populations of *P. maniculatus* is far greater, averaging 6.2% (Gill, 1980). An analysis of restriction sites in mitochondrial DNA from four specimens of Santa Catalina Island populations of *R. megalotis* yielded only one polymorphism out of 78 sites examined, far lower than the number found in sympatric populations of *P. maniculatus* (Ashley and Wills, 1987; Ashley, 1989). Therefore, we believe that the population on Santa Catalina Island also is the result of a recent introduction, although this population has had a greater length of time to become adapted to the environment than has the population on Santa Cruz Island.

With access to the California Islands by land bridge ruled out, other means of transport must be considered. In southern California, rafting has been documented for *Lepus californicus*; one individual was found weak but alive on a kelp raft 63 km from the nearest point on the mainland and 24 km northwest of San Clemente Island (Prescott, 1959). Given the extent of the water barriers between the islands and the mainland, however, chances that the mice rafted to the island are less likely than colonization by human transport (Wenner and Johnson, 1980). The regular transport of supplies and material between the mainland and the islands

by the Chumash and Gabrieleño Indians was extensive and began approximately 9000 years BP when the islands were first settled (King, 1971; Targaglia, 1976; Hudson *et al.*, 1978). The Indians stored their plank canoes in marshes between voyages (Hudson *et al.*, 1978), providing ample opportunity for harvest mice to inadvertently stow away and be transported to the islands. This method of introduction appears to be the most plausible explanation for the presence of *R. megalotis* on the California Channel Islands.

TAXONOMY

In studies of geographic variation, the naming of subspecies is not as important as deciphering the patterns of variation observed within a species. Like Barrowclough (1982:602), we believe that it is possible to identify infraspecific taxa if separate analyses of electrophoretic and morphometric variation “all delimit the same ‘discrete structures’ in multivariate space.” However, in insular situations, where allopatric populations differ in only one character state, the use of a trinomial might not be warranted. We feel that when properly used to “identify those historical geographic units that represent opportunities for sustained evolutionary divergence” (Smith and Patton, 1988:174), the subspecies category is an important taxonomic category that is helpful to the study and understanding of evolutionary processes and models.

In the western harvest mouse, four subspecies (*R. m. catalinae*, *R. m. limicola*, *R. m. longicaudus*, and *R. m. santacruzae*) currently are recognized in southern California (Hall, 1981). With the exception of the two allopatric island populations, there are no discrete geographic barriers to gene flow that coincide with existing subspecies boundaries. Results of the genetic and phenetic analyses presented above indicate that within populations of *R. megalotis* in southern California there are no historical geographic units that warrant subspecific recognition. Rather, there exists broad phenetic overlap among the samples, suggesting that only gradual, small-scale phenetic change occurs among *R. megalotis* populations in mainland southern California.

In examining patterns of geographic variation, it is important to ask whether the observed geographic variation is the result of genetic change due to genetic drift, whether it is a plastic response to local environmental conditions, or whether it represents fundamental adaptive genetic change. Patton and Brylski (1987) have shown that body size in *Thomomys bottae* is an ecophenotypically plastic character, whereas shape differences are the products of long-term evolutionary divergence. In the case of *R. megalotis* on Santa Cruz and Santa Catalina islands, there has been a divergence from mainland populations in size but not in cranial shape. The lack of any underlying shape difference and the fact that there are no substantive genic criteria distinguishing the island samples from the mainland sam-

ples suggests that populations of *R. megalotis* in southern California are of one genetic stock. The size increase in the two island populations may be a phenotypic response to the unique environmental conditions present on the islands and not the product of long-term evolutionary divergence. The San Clemente Island population, which von Bloeker (1967) suggests was inadvertently introduced to the island during the 1930s in shipments of baled hay from San Diego County, has not shown a comparable shift in body size similar to that seen in the other two island populations. This suggests that harvest mice have been isolated on Santa Cruz and Santa Catalina islands for a longer period of time than they have been on San Clemente Island.

In the absence of any substantive genic or morphologic breaks across the geographic range of the western harvest mouse in southern California, we conclude that only one subspecies should be recognized. We recommend that the following nomenclatural adjustments be made. The name *R. m. longicaudus* (Baird, 1857), which has priority, would apply to all harvest mouse populations in southern California west of the foothills of the San Gabriel, San Bernardino, and San Jacinto mountain ranges, as well as on the Channel Islands. Following is a revised synonymy for this species in the southern California region.

Reithrodontomys megalotis longicaudus (Baird)

Reithrodon longicauda Baird, 1857:451 (orig. desc.).
Ochetodon longicauda: Coues, 1874:186.
Reithrodontomys pallidus Rhoads, 1893:835 (orig. desc.).
Reithrodontomys longicauda: Allen, 1895:129.
Reithrodontomys longicauda pallidus: Allen, 1895:131.
Reithrodontomys klamathensis Merriam, 1899:93 (orig. desc.).
[*Reithrodontomys*] *longicaudus*: Elliot, 1901:151.
Rhithrodontomys catalinae Elliot, 1904:246 (orig. desc.).
Reithrodontomys megalotis longicauda: Mearns, 1907:464.
Reithrodontomys catalinae: Howell, 1914:40.
Reithrodontomys megalotis klamathensis: Grinnell, 1913:303.
Reithrodontomys megalotis longicaudus: Howell, 1914:33.
Reithrodontomys megalotis catalinae: Grinnell, 1913:304.
Reithrodontomys megalotis limicola von Bloeker, 1932:133 (orig. desc.).
Reithrodontomys megalotis santacruzae Pearson, 1951:366 (orig. desc.).

DIAGNOSIS. *Reithrodontomys m. longicaudus* can be characterized as dark and small in size (total length, 124–163 mm), except for the populations on Santa Cruz and Santa Catalina islands, which

are large bodied (total length, 152–178 mm). The color of the upperparts is mixed-blackish and ochraceous-buff with black predominating on the back of the neck and shoulders; the ventral surfaces are grayish white with a wash of ochraceous-buff, especially in the pectoral area. The sides are a brighter ochraceous-buff than the back, whereas the ears are the same color as the back with a wash of ochraceous hairs on their inner surfaces. The tail is bicolored, hair brown above and grayish white below. Color variation in *R. m. longicaudus* is considerable across the geographic range of the subspecies, with summer and winter pelages decidedly different. Lacking much of the black on the dorsal surface, fresh summer pelage is noticeably paler than that of fresh winter pelage.

COMPARISONS. *Reithrodontomys m. longicaudus* exhibits considerable geographic variation both in color and in size of skull. According to Howell (1914), this subspecies can be distinguished from *R. m. megalotis* by its small size and somewhat darker (more heavily washed with black), more intense colors. These two subspecies intergrade in a number of places along the edge of the deserts in southern California (Howell, 1914). Western harvest mice on Santa Cruz and Santa Catalina islands can be distinguished from other populations of *R. m. longicaudus* only by their slightly larger size. According to von Bloeker (1937), *R. m. distichlis* (from coastal marshes at Monterey Bay) can be distinguished from *R. m. longicaudus* by the former's smaller size and average darker dorsal coloration. The taxonomic validity of *R. m. distichlis* has been questioned by Pearson (1951), who could not distinguish specimens assigned to this taxon from upland *R. m. longicaudus* in the area. A more detailed assessment of the genetic and morphological characteristics of purported *R. m. distichlis* populations may find that, as for *R. m. limicola*, the characters originally used to identify this taxon are too slight and inconsistent to warrant its continued recognition.

RANGE. *Reithrodontomys megalotis longicaudus* is a broadly distributed subspecies of the western harvest mouse that ranges from southwestern Oregon southward throughout most of western California and along the coast into northwestern Baja California to about 32° N latitude (Howell, 1914; Hall, 1981). In California, *R. m. longicaudus* inhabits the greater part of western California east to the foothills of the Sierra Nevada, San Bernardino, and San Jacinto ranges, whereas *R. m. megalotis* can be found east of these mountain ranges, including most of the Great Basin, Mohave Desert, and Sonoran Desert regions of the state (Grinnell, 1933). Based on the results of this study, we are also including the introduced population of western harvest mice on San Clemente Island, as well as the harvest mice found in the coastal salt marshes of southern California and on Santa Cruz and Santa Catalina islands, within the range of *R. m. longicaudus*.

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APPENDIX

List of Specimens Examined

Localities for specimens of *Reithrodontomys megalotis longicaudus* examined in the morphometric and allozymic analyses are listed below by number, with acronyms in parentheses, and are indicated on the map (Fig. 1). Sample sizes for each analysis are indicated by numbers in parentheses as follows: m = morphometric sample, e = allozymic sample. A listing of the complete names for collections in which specimens are housed can be found in the acknowledgments; additional specimens were exam-

ined at the Natural History Museum of Los Angeles County (LACM) and the Santa Barbara Museum of Natural History (SBMNH). Frozen tissues are deposited in the Frozen Tissue Collection at the Natural History Museum of Los Angeles County. Voucher specimens for frozen tissues are deposited at LACM, SBMNH, UCSB, and the University of Kansas. All localities listed are in California.

Locality 1 (SCRUZI; m = 28, e = 20). Santa Barbara Co., Santa Cruz Island: end Central Valley, NW airstrip (m = 2 LACM, 1 SBMNH; e = 3); E end Central Valley, E end airstrip (m = 3 SBMNH; e = 2); E end Central Valley, orchard E airstrip (m = 1 SBMNH; e = 1); E end Central Valley 0.1 mi. S dump (m = 2 LACM; e = 2); Prisoners' Harbor (m = 6 MVZ, 5 LACM, 7 SBMNH; e = 12); 1 mi. S Prisoners' Harbor (m = 1 LACM).

Locality 2 (SCATI; m = 94, e = 15). Los Angeles Co., Santa Catalina Island: no specific locality (m = 3 LACM, 12 MVZ); 2 mi. W Avalon (m = 1 SBMNH); Avalon (m = 1 MVZ, 3 SBMNH); 0.5 mi. SW Avalon (m = 1 SBMNH); Big Fisherman's Cove (m = 1 MVZ); Bulrush Canyon (m = 7 SBMNH; e = 4); Campo Blanco Canyon, below El Rancho Escondido (e = 1); Catalina Harbor (m = 4 SBMNH); lower Cottonwood Canyon, 100 m below Cottonwood Dam (m = 1 SBMNH); Cottonwood Canyon, 0.7 km E Cottonwood Dam (m = 1 SBMNH); Eagles Nest (m = 12 UCLA); upper Fern Canyon, 1.6 km above jct. Cottonwood Canyon (m = 1 SBMNH; e = 2); bluff above Indian Head Point, 0.6 mi. SW Little Harbor, 450 ft (e = 1); Johnson's Landing (m = 15 LACM); Middle Canyon, 0.25 mi. W Eagles Nest Lodge (m = 1 SBMNH); Middle Canyon, 0.1 km W Eagles Nest (m = 2 SBMNH); Middle Canyon, jct. Middle Ranch Road and Ben Weston Road (m = 1 SBMNH); Middle Canyon, S side Thompson Reservoir, 50 yd E spillway (m = 8 SBMNH; e = 4); Middle Ranch, 1100 ft (m = 5 LACM, 3 SBMNH); Middle Ranch Canyon, slope NNW bunkhouse (e = 1); Middle Ranch Canyon, plant propagation facility, E end Thompson Reservoir (e = 2); Middle Ranch Canyon, lower end Thompson Dam (m = 1 SBMNH); White's Landing (m = 10 LACM).

Locality 3 (PTMUGU; m = 50, e = 20). Ventura Co.: Ormond Beach (m = 23 LACM); Pt. Mugu (m = 4 LACM); Pt. Mugu salt marsh (m = 3 LACM); Pt. Mugu Naval Air Station, Beach Road along Dirt Pole Line Road (m = 1 SBMNH; e = 1); Pt. Mugu Naval Air Station, *Salicornia* marsh NW Bldg. 736 to W of S 6th St (m = 2 LACM; e = 2); Pt. Mugu Naval Air Station, *Salicornia* marsh between bldgs. 735 and 738 (m = 8 SBMNH, 1 LACM; e = 9); Pt. Mugu Naval Air Station, end Tacan Road (m = 8 SBMNH; e = 8).

Locality 4 (DELREY; m = 11, e = 15). Los Angeles Co.: Ballona Wetlands (e = 15); Del Rey (m = 2 SBMNH); Playa del Rey salt marsh (m = 8 LACM, 1 UCLA).

Locality 5 (ANAHAM; m = 17, e = 15). Orange Co.: Anaheim Bay salt marsh (m = 2 LACM); Seal Beach National Wildlife Refuge *Salicornia* marsh (m = 8 LACM, 7 SBMNH; e = 15).

Locality 6 (NEWPR; m = 12, e = 11). Orange Co.: Newport Bay (m = 1 SBMNH); Upper Newport Bay Ecological Reserve (m = 6 LACM, 5 SBMNH; e = 11).

Locality 7 (STYNEZ; m = 19, e = 18). Santa Barbara Co.: mouth Santa Ynez River, salt marsh (m = 9 LACM, 10 SBMNH; e = 18).

Locality 8 (NSBARB; m = 25, e = 14). Santa Barbara Co.: Bixby Ranch, ocean bluff adj. Black Canyon, approx. 1 mi. N Pt. Conception (e = 4); Bixby Ranch, jct. Government Point and Point Conception roads, approx. 1 mi. E Pt. Conception (e = 5); Canada del Cojo (m = 2 SBMNH); ¼ mi. W Government Point (e = 1); 1.5 mi. N La Purisima

Mission, 600 ft ($m = 3$ MVZ); La Purisima Mission, 3.4 mi. NNE Lompoc ($e = 3$); Los Alamos, Las Flores Ranch ($m = 1$ SBMNH); Pt. Arguello ($m = 7$ LACM); N Vandenberg Air Force Base, adj. S20, 1 mi. SW jct. Hwy 1 ($m = 2$ SBMNH); S Vandenberg Air Force Base ($m = 8$ SDMNH); S Vandenberg Air Force Base, S jct. Old Coast Road and SLC-4 Road, near Spring Canyon ($m = 1$ SBMNH; $e = 1$); S Vandenberg Air Force Base, N side Red Roof Canyon, 0.1 mi. E jct. Coast Road ($m = 1$ SBMNH).

Locality 9 (DEVERO; $m = 20$, $e = 13$). Santa Barbara Co.: Devereux Slough ($m = 5$ LACM, 5 SBMNH, 8 UCSB); Devereux Slough, NW corner ($e = 2$); Devereux Slough, NE arm adj. horse corrals, Coal Oil Point Reserve ($e = 5$); Devereux Slough, NE corner below Married Student Housing ($e = 1$); Devereux Slough, E arm near Devereux School ($e = 2$); University of California, Santa Barbara, E Side Devereux Slough ($e = 3$); University of California, Santa Barbara, Stork Campus wetlands ($m = 2$ UCSB).

Locality 10 (GOLETA; $m = 25$, $e = 13$). Santa Barbara Co.: Lowlands SW jct. Los Carneros and Mesa roads ($m = 6$ UCSB); Goleta Slough ($m = 1$ SBMNH, 18 UCSB; $e = 10$); University of California, Santa Barbara, Stork Campus W of Los Carneros Road ($m = 1$ UCSB); University of California, Santa Barbara, Stork Campus SE jct. Los Carneros and Mesa roads ($e = 3$).

Locality 11 (SSBARB; $m = 29$). Santa Barbara Co.: near Gaviota ($m = 6$ UCLA); Goleta, middle fork Las Vegas Creek, 1.2 mi. N jct. La Goleta Road ($m = 1$ UCSB); 0.35 mi. E Greenwell Ave off Via Real ($m = 1$ SBMNH); near Hendry's Beach, Santa Barbara ($m = 1$ UCSB); 4.7 mi. N Hwy 101 off Refugio Pass Road ($m = 1$ SBMNH); Mission Creek along Tunnel Road, 1200 ft ($m = 1$ SBMNH); Mora Mesa, Central Canyon ($m = 1$ UCSB); 3 mi. SW Old Mission Santa Barbara ($m = 1$ SBMNH); Old San Marcos Road, 1 mi. N Cathedral Oaks Road ($m = 1$ SBMNH); 1 mi. SW Painted Cave area, 1200 ft ($m = 1$ SBMNH); Santa Barbara, 1166 Palomino Road, 750 ft ($m = 11$ SBMNH); 5 mi. W Santa Barbara, Hope Ranch ($m = 2$ UCLA); 4 mi. E Santa Barbara, 600 ft ($m = 1$ LACM).

Locality 12 (CARPUP; $m = 28$, $e = 12$). Santa Barbara Co.: Arroyo Paredon, 2 mi. N mouth Carpinteria Slough ($e = 12$); 2 mi. N Carpinteria ($m = 2$ UCLA); 2 mi. E by N of Carpinteria ($m = 8$ MVZ); Carpinteria ($m = 2$ SDMNH); summit El Rincon Hill ($m = 2$ LACM); Higgins Ranch, Carpinteria ($m = 4$ LACM); Santa Ynez Mountains, 3.5 mi. NW Carpinteria ($m = 1$ LACM); upper Hancock Ranch, Mendoza Canyon ($m = 9$ LACM).

Locality 13 (CARPIN; $m = 24$, $e = 14$). Santa Barbara Co.: Carpinteria Marsh ($m = 7$ LACM, 7 SBMNH; $e = 14$); El Estero salt marsh, 1 mi. W Carpinteria ($m = 3$ LACM, 1 UCSB); Sandyland Dunes, 1.5 mi. W Carpinteria ($m = 2$ MVZ); Sandyland Slough, Carpinteria ($m = 2$ MVZ, 2 UCSB).

Locality 14 (LACOU; $m = 18$, $e = 11$). Los Angeles Co.: 0.5 mi. NW El Segundo ($m = 1$ MVZ); Hollywood ($m = 1$ UCLA); Pasadena ($m = 2$ UCLA); Puente Hills, near Erras Ranch ($m = 1$ UCLA); Rancho Palos Verdes, Que Viento Canyon ($m = 10$ LACM; $e = 11$); San Dimas ($m = 2$ UCLA); Santa Monica ($m = 1$ SDMNH).

Locality 15 (SCLEMI; $m = 14$). Los Angeles Co., San Clemente Island: China Canyon, 200 ft ($m = 4$ LACM); Horse Beach Cove ($m = 8$ LACM); Horse Beach Point ($m = 1$ LACM); Pyramid Cove, salt marsh ($m = 1$ LACM).

Locality 16 (ORANGE; $m = 20$, $e = 10$). Orange Co.: Harding Ridge Road, 5 mi. E Tucker Wildlife Sanctuary, 4000 ft ($m = 1$ LACM); 4.1 mi. N Laguna Beach, Laguna Canyon Road ($m = 7$ LACM); 15 mi. NE Orange, 450 ft ($m = 3$ SDMNH); Starr Ranch, Bell Canyon Road (T6S, R7W, Secs. 25 and 36) ($m = 6$ LACM, 2 SBMNH; $e = 9$); Trabuco Canyon Road, 2 mi. N, 16 mi. E El Toro ($m = 1$ LACM; $e = 1$).

Locality 17 (SDIEGO; $m = 23$, $e = 7$). San Diego Co.: Oceanside ($m = 8$ SDMNH); San Onofre ($m = 1$ SDMNH); mouth Santa Margarita River ($m = 4$ LACM; $e = 7$); Santa Margarita area, Camp Pendleton ($m = 1$ SDMNH); Solano Beach ($m = 1$ SDMNH); mouth Tijuana River ($m = 8$ SDMNH).